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Metapopulation Dynamics and
Landscape Ecology

John A. Wiens

I. INTRODUCTION

The fusion of metapopulation studies and landscape ecology should make for an exciting scientific synthesis (Hanski and Gilpin, 1991)

The synthesis of metapopulation studies and landscape ecology anticipated by Hanski and Gilpin has barely yet begun. There are at least two reasons for this (Wiens, 1995a). First, as many of the chapters in this volume illustrate, metapopulation theory continues to be tied to a view of spatial patterning of environments in which patches are embedded in a featureless background matrix. Second, landscape ecology seems still to be in the process of defining what it is about and describing complex spatial patterns, but it has not developed much theory to deal with spatial patterning. By focusing on some shared areas of interest, perhaps the synthesis of these disciplines can be accelerated.

In this chapter, I consider the relationship between the emerging (but yet immature) discipline of landscape ecology and the emerged (but perhaps adolescent) discipline of metapopulation dynamics. I will argue that considerations of metapopulation structure may often be incomplete unless they are framed in the context of the underlying landscape mosaic.

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II. APPROACHES TO PATCHINESS

Ecologists have always known that nature is patchy and heterogeneous, even if, as a discipline, they have not treated it so. Indeed, in areas used by humans occur a sharply defined landscape mosaic, and the patchiness of the landscape mosaic is especially evident in such environments. Even in more natural settings, however, habitats are heterogeneous at virtually any scale of resolution. Although patch boundaries in such situations may sometimes be indistinct gradients rather than sharp discontinuities (Wiens, 1992b), the spatially variable nature of such systems is not in doubt. In this chapter I will follow the convention that has become widespread in ecology of referring to such systems in the rubric of "patchiness," even though "patches" are not always evident in nature. Dealing with such spatial heterogeneity has been a major challenge in both empirical and theoretical ecology. Faced with the daunting complexity of spatial patterns in the real world, field ecologists historically tended to focus on patterns (e.g., warblers, woodrats) or aggregated spatial patterns (e.g., density, diversity indices of heterogeneity or dispersion. More recently, it has become fashionable to map spatial patterns at broad scales using geographic information systems and spatial statistics, but the link between such technologies and ecologically important questions is not always apparent.

There are two main branches of analytical models and theory; if it is viewed explicitly (i.e., by location) rather than averaged as "noise." As a consequence, many theoreticians concerned with heterogeneity have contented themselves with simple models in which spatial patterning is collapsed into patches and an ecologically neutral "matrix" (Kareiva, 1990b; Wiens, 1995a). Such patch-matrix theory is usually spatially implicit (Hanski, 1994c), in that the spatial pattern of patches is not explicitly modeled. In such models, interesting dynamics occur in the patches, which are usually considered to be internally homogeneous; the matrix is viewed as inhibiting interactions among patches (e.g., migration, colonization, gene flow, prey discovery by predators).

Traditional metapopulation theory is an elaboration on this patch-matrix theme. Levine's metapopulation model (1979; Hanski, this volume) considered the behavior of a species occupying a landscape in which patches are occupied by the species and unoccupied locations in a background matrix. As metapopulation modeling has progressed, however, details about patch sizes, patch clumping, individual movement capacities, local patch dynamics, and explicit patch locations have been incorporated (Hanski, 1994a,c; see Hanski, this volume; Gyllenberg *et al.*, 1994, this volume). Another theory deals with the dynamics of populations occupying a patchy environment (Wiens, 1976; Levin, 1976; Kareiva, 1990b; Shorrocks and Slevin-lund, 1990). Another approach to heterogeneity has focused on the dynamics of the patches themselves. Although the spatial pattern of some patches, such as the islands considered in island biogeography theory, may be relatively static in ec-

ological time, the patch structure of most environments is not. Patches are destroyed and generated by disturbances at multiple scales. They undergo change through successional development. These "patch dynamics" (Pickett and White, 1985) produce changes in the spatial patterns and relationships of patches in a landscape. In this chapter, I will review the history of patch dynamics and the approaches (patch demography, Lotka and Plank, 1936; Turner, 1989; Hanski *et al.*, 1990) that have been used to study patch dynamics. I will also review the approaches (e.g., Fahrig, 1990). Most of this work has followed the patch-matrix conceptualization of spatial patterns.

In the recent emergence of landscape ecology as a discipline (Risser *et al.*, 1984; Turner *et al.*, 1989; Turner, 1989a; Wiens, 1992a; Wiens *et al.*, 1993; Hobbs, 1995), offers the opportunity to adopt a more realistic, spatially textured view of heterogeneity. In landscape ecology, the "matrix" is itself spatially structured, and spatial relationships play an active role in determining the dynamics within the patches of interest. Patches are viewed as components in a landscape mosaic, and the spatial pattern of patches is itself a component of the landscape mosaic. The composition and dynamics of other elements of the landscape mosaic (Wiens *et al.*, 1993; Arden, 1994; Wiens, 1995a, 1996a).

III. WHAT IS LANDSCAPE ECOLOGY?

One of the first tasks of an emerging discipline is to define its core and itself. "Landscape" has been defined as "a heterogeneous land area composed of a cluster of interacting ecosystems" (Forman and Godron, 1986), "a mosaic of heterogeneous land forms, vegetation types, and land uses" (Ulrich *et al.*, 1987), or "a spatially heterogeneous area" (Turner, 1989). Accordingly, "landscape ecology" is "a study of the spatial arrangement of ecosystems and the processes of integration of ecosystem structure and function at the landscape scale" (Bojór *et al.*, 1994). It emphasizes "broad spatial scales and the ecological effects of the spatial patterning of ecosystems" (Turner, 1989) and "offers a way to consider environmental heterogeneity or patchiness in spatially explicit terms" (Wiens *et al.*, 1993).

If these definitions are a bit nebulous, it may reflect the multifarious historical development of landscape ecology and continuing uncertainty or disagreement over what it is really about. Landscape ecology began in northern Europe during the 1960s as an outgrowth of holistic ecology with human geography, with influences from landscape architecture, landscape ecology, and other disciplines (Turner, 1989; Wiens *et al.*, 1993; Fahrig, 1990; Turner, 1989). In the United States, it was practical and applied: the focus was on the interaction of humans with their environment at a broad (landscape) spatial scale. In the early 1980s, the discipline colonized North America (and other continents, most notably Australia). The

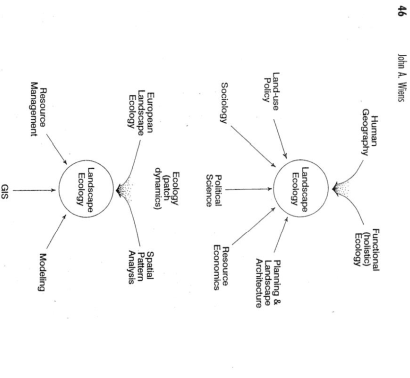


FIGURE 1 Contributions to the historical development of landscape ecology in Europe (top) and North America (bottom).

benchmarks in North America were small and initially somewhat isolated. Perhaps the most influential founder of North American landscape ecology there following the second world war was Robert Turner (Fig. 1, bottom). The conceptual questions asked and approaches used differed considerably. There was a more self-conscious emphasis on concepts (Weins, 1995a), a greater reliance on quantitative procedures (Turner and Gardner, 1991), and an application of the landscape ecology pathways of historical development have led to three rather different views of the primary focus of landscape ecology. Continuing in the European

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tradition, one view portrays landscape ecology as "a new holistic, problem-solving approach to resource management" (Barrett and Bohlin, 1991). It is a synthetic, holistic, human ecology. The second view, which has become most prevalent among ecologists, treats "landscape" as a level of organization (e.g., O'Neill *et al.*, 1988; Turner *et al.*, 1989; Turner and Gardner, 1991; Turner *et al.*, 1994). In the latter case, the questions are often no different from those of landscape ecology (Turner *et al.*, 1989; Turner and Gardner, 1991; Turner *et al.*, 1994). The third view more explicitly emphasizes the structure and dynamics of landscape mosaics and their effects on ecological phenomena (Turner, 1989; Weins *et al.*, 1992). It is a view that has been less well defined than the second, but is based on investigation of landscape dynamics at the regional scale and is more than just spatially explicit ecology, because the patterns and interactions of entire mosaics are the focus of investigations.

This diversity of views suggests that landscape ecology is "a science in search of a theory" and is a discipline in being a young discipline. It is also methodologically immature. In that it lacks a well-defined theoretical framework (Turner, 1989; Weins, 1995a) and tends to be more qualitative than quantitative (Weins, 1992a). Despite all of this, several prevailing themes of landscape ecology have emerged:

- Elements in a landscape mosaic (patches) vary in quality in both space and time. In a landscape patch quality is a continuous variable, but the quality is suitable vs. unsuitable, or patch-matrix) variable. Patch quality can be viewed as a spatially dependent cost-benefit function (Weins *et al.*, 1993; Weins, 1996a).
- Patch edges or boundaries may play critical roles in controlling or filtering flows of organisms, nutrients, or materials over space (Weins *et al.*, 1985; Holland *et al.*, 1992; Turner *et al.*, 1992). Patch edges and boundaries may have important effects on both within-patch and between-patch processes.
- The degree of connectivity among elements in a landscape mosaic has major consequences on patch interactions and landscape dynamics (Ladkovich and Fahrig, 1985; Taylor *et al.*, 1993). How disturbances propagate over a landscape, for example, may be dictated by landscape connectivity as well as by landscape structure (Turner *et al.*, 1989). Connectivity involves much more than simple dispersal.
- Patch context matters. What happens within a patch is contingent on its location, relative to the structure of the surrounding mosaic. A patch of the same habitat may be of quite different quality, depending on the features of adjacent patches (Turner *et al.*, 1992; Weins *et al.*, 1993). Contrary to island biogeography (cf. Janzen, 1983). It is the contextual dependency that requires landscape ecology to be spatially explicit.

IV. HOW IS LANDSCAPE ECOLOGY RELEVANT TO METAPOPULATION DYNAMICS?

To see how these themes may relate to metapopulation dynamics, we must review briefly the essential features of metapopulation theory (see Hanski and Simberloff, this volume). "Metapopulations" have been defined in various ways, but most definitions emphasize the spatial arrangement of local populations and recolonizations of local populations that facilitates long-term persistence of the metapopulation (Levins, 1970; Hanski and Thomas, 1994; Hanski, this volume). The dynamics of local populations are density-dependent within patches but asymmetric among patches, and migration (dispersal) among patches links them together. The spatial arrangement of patches is important because the distance among patch distances (and other spatially uncorrelated sources of population variability) are not important; the dynamics of local populations will be mixed together and they will act as a single large population. On the other hand, if movement among patches is infrequent it may not be adequate to ensure recolonization of habitat patches in which local populations have suffered extinction, dooming the entire metapopulation to extinction (Wiens, 1997).

The contrast between this classical view of metapopulations and a landscape-based view is perhaps most apparent graphically. In a traditional (theoretical) metapopulation, local populations occur in habitat patches in a featureless matrix (Fig. 2A). Not all patches are occupied at a given time, and local populations may go extinct but the extinction and recolonization occur "patches" may vary in size but they do not affect the primary dynamics of the metapopulation model spatially explicit is therefore necessary, but not sufficient, to cast it in a landscape context. In reality, the local populations of a metapopulation occur in habitat patches that are immersed in a complex mosaic of other habitat patches, and the landscape context may affect the dynamics of the metapopulation (Fig. 2B). The matrix may have a complex structure, and the landscape structure may affect the movement of individuals among patches. Consequently, on patch-recolonization probabilities. In a landscape mosaic, inter-patch distances are not Euclidean (e.g., Fig. 2A), but are a complex function of boundary permeabilities and relative patch viscosities to moving organisms (e.g., Fig. 2B; Wiens *et al.*, 1995). Other aspects of metapopulation structure, such as patch extinction probabilities, may also be influenced by landscape structure.

Because very little empirical work that directly links landscape ecology to metapopulation dynamics has been published, I will review the "landscape ecology" literature to see if any movements of individuals beyond their home ranges, or an emigration to a new patch, are not a random process, but are influenced by landscape structure. I will then review the "landscape ecology" literature to see if any movements of individuals beyond their home ranges, or an emigration to a new patch, are not a random process, but are influenced by landscape structure.

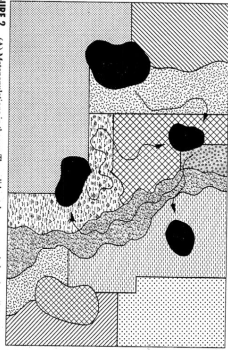
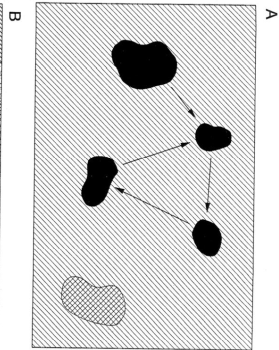


FIGURE 2 (A) Metapopulations in theory. The solid patches are occupied and are linked by inter-patch movement. (B) Metapopulations in reality. The patches are the same, but the "matrix" (the background) is a complex mosaic of different patterns, representing a heterogeneous landscape. The probability that migrating individuals will reach the patches are affected by the spatial configuration of the landscape.

metapopulation dynamics has been rare, a discussion of how the major themes of landscape ecology—spatial and temporal variations in patch quality; boundary effects; landscape connectivity; and patch context—affect the three components of metapopulation dynamics (local extinction, interpatch movement, and recolonization) must necessarily be somewhat abstract and conceptual. It may be useful, therefore, to preface this discussion with a few examples of the effects of landscape structure in the real world. Additional examples are provided by Augenstein (1992), Fahrig and Treeman (1993), and Hobbs (1995).

A. Some Examples of Landscape Effects

Some of the effects of landscape patterns are related to patch characteristics such as patch size or spacing. For example, the size of habitat patches has been shown to affect the persistence of local populations of forest birds (Peterson et al. 1999). The size of patches has also been shown to affect the abundance of insect herbivores (Peterson et al. 1999). The ability to effect the likelihood of recolonization of vacant patches by new clonal fragments (Muller-Landau et al. 1998; Tilman et al. 1998). Both patch size and spacing influenced the use of *Populus balsamifera* (*Populus australis*) of remnant forest reserves in New Zealand (Parker, 1990). Kivari et al. (1999) found that the size of patches had a significant effect on the abundance of large and small birds in New Zealand forests. All fragments less than 100 ha were occupied by large birds, whereas small birds were found in fragments of all sizes. The size of patches also had a significant effect on the abundance of large and small birds in New Zealand forests. All fragments less than 100 ha were occupied by large birds, whereas small birds were found in fragments of all sizes. The size of patches also had a significant effect on the abundance of large and small birds in New Zealand forests. All fragments less than 100 ha were occupied by large birds, whereas small birds were found in fragments of all sizes.

of Chlorella, and other microalgae, may also be the result of the high degree of variability in the response of the microalgae to the proportion of the patch boundary that is bordered by open fields (Kutner *et al.* 1996). Gysel and Gysel (1978) found that the abundance of grasshopper beetles increased as the boundary between forest and grassland increased, and they suggested that herbivores might be drawn to the edge as nesting habitat because of greater food availability there (Kutner *et al.* 1996). Anderson (1992) found that grasshopper beetles increased in abundance as the proportion of the patch boundary that was bordered by open fields increased. The results of the present study suggest that the response of grasshopper beetles to the proportion of the patch boundary that is bordered by open fields is not a simple function, as in a well-circumscribed way by attracting individuals to areas in which predation losses are great (Gysel and Gysel 1978). Predation losses at habitat boundaries may be a function of the surrounding habitat (Whitlow 1988). Anderson (1992, 1995, 1996), on the landscape context of studies at a local temporal scale, found that grasshopper beetles were more abundant in habitats with a greater proportion of open fields, presumably due to predators being attracted to habitats with more open edges. Any function, such as in a well-circumscribed way by attracting individuals to areas in which predation losses are great (Gysel and Gysel 1978), that would result in a response such that predation losses are great (Gysel and Gysel 1978), Predation losses at habitat boundaries may be a function of the surrounding habitat (Whitlow 1988). Anderson (1992, 1995, 1996), on the landscape context of studies at a local temporal scale, found that grasshopper beetles were more abundant in habitats with a greater proportion of open fields, presumably due to predators being attracted to habitats with more open edges. Any function, such as in a well-circumscribed way by attracting individuals to areas in which predation losses are great (Gysel and Gysel 1978), that would result in a response such that predation losses are great (Gysel and Gysel 1978),

pecially where populations are subdivided among many small habitat patches and predation risk is significant.

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B. Movement and Migration

Individual movement is the monoprotic uniting element in various population dynamics and landscape ecology (Samuelson et al. 1991; Krebs 1992a, 1995; Wiens et al. 1993; Ims, 1993). Moreover, how fast and how far organisms move impacts a species on the environment, highly vagile animals integrate best the ecologically very broader scales than do sessile organisms and therefore perceive the environment with a coarser filter or "grain" (Wiens, 1983; Fahrig and Pabst-Henrich, 1988; Kodlar and Wiens, 1990; De Roos et al. 1991; Wiens and Shapley, 1991). In the context of any field study or modeling exercise, then, the mean and shape of a species' migration function determines the scale(s) at which population responses to environmental patches must be investigated.

In the tradition of island biogeography theory, a metapopulation model assumes that local populations are subject to stochastic extinction and recolonization possibilities (e.g., Hanski, 1994a). The falling and Pahlsson (1998) simulation studies of the effects of the spatial configuration of patches on population abundances in a metapopulation, for example, indicated that migration rates, rather than migration rates alone (or demographic features such as birth and death rates), were critically important, especially when interpatch distances were great. In contrast, when Liu et al. (1995) modelled Bachman's sparrow (*Ammodramus*) population dynamics, they found that demographic parameters were more important than mortality during dispersal (although not necessarily dispersal

rate or distance). These differences may stem from differences in model structure, but they may also reflect basic differences in the life histories of the organisms modeled.

Transition metapopulation models usually do not consider the details of movement in even an abstract sense. Movement is modelled as transition probabilities among cells in a grid (e.g. *Levins et al.* 1995) or movement rates and distances are simply specified or are drawn from frequency distributions. Whether movement through the matrix between patches is directed (e.g. *Fig. 2a*) or not (e.g. *Fig. 2b*) is not considered, even though the difference (Turchin, 1989; *Janzen et al.* 1992a) is not trivial. Even though the differences among these movement patterns can produce substantial differences in the probability of encountering a patch in the matrix, this is especially true if migration rates are low or if the number of individuals available to migrate is quite limited (as may occur when local populations are small).

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To make such an individual-based conceptualization of mosaic movements relevant to metapopulation dynamics, it must be extended to the scale of population rather than individual patches (Fig. 3B). In simple terms, this is a matter of shifting the scale from that of movements and patches defined by individual home ranges to the broader-scale movements of populations (i.e., migration) and the scale of patchiness represented by interactions within a local population (i.e., nodes in a metapopulation). Exactly how the transition from individual movements to population distribution and interactions should be accomplished is one

Figure 3 consists of two panels, A and B. Panel A, labeled 'Individual', shows a sequence of grey circles representing spatial configurations of a male pupfish over time. An arrow indicates the movement path from one configuration to the next, eventually leading to a black circle representing the final position. Panel B, labeled 'Population', shows a similar sequence of grey circles, but with arrows indicating the probability of movement from each configuration to a final position (black circle). The arrows are labeled with probabilities $q_1, q_2, q_3, q_4, q_5, q_6, q_7, q_8, q_9, q_{10}$ and p .

of the most vexing problems confronting a metapopulation-landscape synthesis. It is part of the more general problem of translating across scales in ecology (Wiens, 1989a; King, 1991; Rastetter *et al.*, 1992).

My colleagues and I have used systems of small animals (fish) moving through parallel "microchannels" as experimental model systems (Greer et al., 2002). We used these systems to investigate how neurons are affected by stress, structure, and function. We used a system of small animals (fish) moving through parallel "microchannels" as experimental model systems (Greer et al., 2002). We used these systems to investigate how neurons are affected by stress, structure, and function. We used a system of small animals (fish) moving through parallel "microchannels" as experimental model systems (Greer et al., 2002). We used these systems to investigate how neurons are affected by stress, structure, and function.

effects on local movements and that these effects differed among *E. leucolus* species. In the case of *E. leucolus*, the effects of patch quality on movement were in areas dominated by bare ground and by continuous low grass cover than in more heterogeneous areas that contained castor oaks or shrubs, and larger beetle species exhibited greater displacements in a given habitat type than did smaller beetles. The relative complexity (fractal dimension) of the movement pathways, however, was not affected by habitat type or species. On the other hand, the relative complexity of movement pathways of grasshoppers over a broader mosaic, relative to that of beetles, was affected by habitat type, at least at the 25 m scale. The relative complexity of movement pathways of grasshoppers over a broader mosaic, relative to that of beetles, was affected by habitat type, at least at the 25 m scale. The relative complexity of movement pathways of grasshoppers over a broader mosaic, relative to that of beetles, was affected by habitat type, at least at the 25 m scale.

These results were confirmed at relatively fine, "within patch" scales and recorded how individual animals responded to landscape patterns. To determine how such movements might translate into patterns of population distribution at broader spatial scales, With and Chitt (1995) used a cell-based simulation model to project the dispersion patterns of populations of grasshoppers over a broader mosaic. Individuals moved within a cell of a given habitat type according to the transition probabilities of that habitat type. The model was run for 1000 iterations, and the resulting patterns of population distribution were compared to the patterns of grasshopper movement recorded in the field. According to a specified transition probability (this corresponds to the between-patch component, ϕ , of Fig. 3B). The landscape mosaic was dominated (65% coverage) by a single habitat type. Under certain specifications of transition probabilities, a large species, *Xanthippus corallipes*, moved rapidly through this cover type. As a result, the population distribution was highly fragmented. A smaller species, *Podisus debilis*, was much more sedentary and preferred a habitat comprising only 5% of the landscape. Given its low vagility, there was a low likelihood of individuals of this species locating and aggregating within cells of the relatively rare, preferred habitat. The model simulations suggested that the distribution of this species was highly fragmented, and that the distribution of the more sedentary species was more continuous. In fact, in the field both species exhibited the general dispersion patterns predicted by the model.

How do these observations and model analyses of patch-specific movements relate to the four components of landscape ecology (patch quality, boundary effects, patch context, and connectivity)? The differences in within-patch movement patterns of the two beetle species, relative to the differences in their population distributions, suggest that the value of transition probabilities between patch types indicates that knowledge of within-patch movement patterns by itself is not adequate to predict broad-scale population distributions. Something else is needed. The most likely factors affecting the transition from individual, within-patch movements to population distribution over a landscape are patch boundary effects and the influence of patch context. Individual beetles react behaviorally to the patch

boundary itself, the likelihood of moving from one patch to another will be affected. If patch context is important, then the mosaic distribution pattern that is beyond a given patch boundary will further modify transition probabilities. Landscape models over movement patterns have yet to receive detailed attention in other models or field studies. Moreover, all of these approaches consider the structure of the landscape mosaic to be fixed; patch dynamics in time and space are not considered (and further computational complications) to the research program.

One aspect of landscape structure that is implicit in the spatial arrangement of mosaic elements and the transition probabilities among them is connectivity. Landscape connectivity refers to the degree to which the landscape facilitates or impedes movement among patches (Taylor *et al.*, 1993). Corridors of similar habitat type, such as riparian corridors, have been shown to facilitate movement (Harris, 1992), but distribute habitat patches among which individuals move are high may also result in high connectivity. Through the patterns of connectivity that characterize a landscape, movement pathways are directed in spatially non-random manners (Fig. 2B), which can either increase or decrease the likelihood that movement among specific patches in the landscape (e.g., subpopulations in a metapopulation) will occur.

Connectivity is related to the coverage of a given habitat type in the landscape, but the relationship is strongly nonlinear. If a continuous habitat is broken into fragments by habitat conversion, the initial effects are due primarily to the loss of habitat coverage alone. As coverage drops below some threshold value, however, the effects of patch isolation begin to be more important. In landscapes with very low coverage of a given habitat type, the effects of patch isolation are in a rapidly increasing distance between habitat patches and even greater isolation effects (Fig. 4). For example, Auldren (1994) found that habitat loss was a good predictor of fragmentation effects on birds and mammals in landscapes with >50% coverage of suitable habitat, but in more highly fragmented landscapes the threshold effects were more important. Such threshold effects have been used by percolation theory. In simple percolation models, a landscape mosaic is divided into suitable and unsuitable habitat patches (cells) that are distributed over the landscape at random, with a specified coverage or proportion, p , of the suitable patches (Gantner *et al.*, 1987, 1989). Above some critical threshold, p_c , cells of the suitable habitat are connected, and the landscape is said to be "percolating." Below this threshold, connectivity is high (O'Neill *et al.*, 1988). For a random landscape in which organisms move only to adjacent (but not diagonal) cells, p_c has a value of 0.5928. If the landscape pattern is generated using a nonrandom algorithm (e.g., fractal cutting; Laveore *et al.*, 1995; With *et al.*, in press), the value of p_c is different. In general, the value of p_c is lower for landscapes with changes in the movement patterns to allow individuals to move to any adjacent cell or to cross

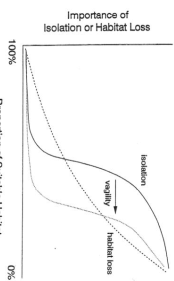


FIGURE 4. A hypothetical relationship between the proportion of suitable habitat in a landscape and the importance of isolation and habitat loss. As the proportion of suitable habitat decreases, the importance of isolation increases monotonically. The effects of patch isolation (the amount of landscape connectivity) are relatively unimportant when the proportion of suitable habitat is small, but become increasingly important as the proportion of suitable habitat increases. The importance of habitat loss increases monotonically with the proportion of suitable habitat. The importance of vagility (the ability of individuals to move among patches) is unimportant when the proportion of suitable habitat is small, but becomes increasingly important as the proportion of suitable habitat increases. The importance of vagility will move this threshold to lower coverage values of the suitable habitat.

gaps, where suitable cells are not immediately adjacent (Dale *et al.*, 1994; Pearson *et al.*, 1996). Field experiments with *Erodia* beetles moving through random landscapes (Wiens *et al.*, in press) indicated a threshold change in movement patterns when coverage of grass in a bare-ground matrix increased from 0 to 20%. Changes in either the spatial pattern of the landscape or the scale over which individuals move can affect the importance of isolation and habitat loss. For example, mean dispersal distance (e.g., the grasshoppers studied by With and Crist, 1995) may also affect the location of a percolation threshold (Fig. 4), as Fahrig and Merriam (1985) also suggested in a somewhat different context. Details of the spatial pattern of the landscape and the scale over which individuals move are likely to be important in determining the importance of isolation and habitat loss.

Most models that link animal movements to landscape structure assume that movement parameters are fixed species traits and that migration can adequately be represented using average vagility. Individuals do vary in movement characteristics, and the effects of this variability on the importance of isolation and habitat loss may be important. For example, Lertz and Doherty (1994) found that created (i.e., *Pinus creata*) young dispersed 1 week later from small, isolated pine stands than did those in large pine forests.

Chicks from second broods were also more likely to disperse into less suitable habitat fragments than were young from first broods. Collectively, these more realistic models suggest that dispersal behavior is not simply a fixed trait, but can be integrated into winter flocks, which would affect their overwinter survival and abilities. In another vein, the simulation studies of Giddaway *et al.* (1994) suggested that variability among individuals could markedly increase the rate of spread of a population, even if only a few individuals in the population migrated rapidly. The prospect that individual movement behavior may be facultatively adjusted to the spatial pattern of the landscape is an important consideration for habitat patches (Mantel *et al.*, 1995; Fahrig and Merriam, 1994) may further complicate attempts to model migration dynamics in heterogeneous landscapes. Nonetheless, it is apparent that the complex interplay between fine-scale movement patterns, broad-scale migration dynamics, and the nonlinear effects of landscape mosaic structure may have fundamentally important effects on the inter-patch movement that lie at the heart of metapopulation dynamics.

C. Local Extinction and Recolonization

In addition to interpatch movement, the extinction of local populations in habitat patches and the subsequent recolonization of those patches are what drive metapopulation dynamics. The importance of these processes is emphasized by the stochastic dynamics that characterize small populations. Deterministic local habitat changes, however, can produce patch dynamics in the landscape that also result in the extinction of local populations (Thomas, 1994). If this is the case, the local patch environment may remain unsuitable for some time after extinction, even if the landscape mosaic is otherwise suitable. The importance of this process on how well the organisms can recolonize the landscape is likely to be important. Because the location of suitable patches may be unpredictable in time as well as in space, how organisms move through the landscape mosaic and the scales on which they perceive environmental patchiness become all the more important. The history of interpatch movement of suitable habitat patches through a landscape mosaic also influences extinction and recolonization probabilities. The degree to which a patch is connected to other suitable areas or is isolated may have little direct effect on extinction, although it may influence the immigration flow and therefore determine the magnitude of the "rescue effect" (Brown and Kodric-Brown, 1977). Colonization, on the other hand, is clearly related to the interpatch movement of individuals. The importance of this process is emphasized by the fact that the connectivity of habitats in the landscape. If fragmentation alters the landscape so that the interpatch movement of individuals may be disrupted, the migration patterns of a species, metapopulation dynamics may be disrupted. To some degree, this situation characterizes the Chuvash tundra in Finland (Hanski *et al.*, 1993).

D. When is a Landscape Approach Necessary?

In all but a few situations, landscapes, rather than patches in a featureless matrix, are reality. Given this, one might conclude that any attempt to model or understand the dynamics of a system does not explicitly include landscape reality. Good theory simplifies in a way that does not violate reality too much, while incorporating its essential features. In this sense, patch-matrix theory represents a significant improvement over theories based on spatial homogeneity (Wiens, 1995a). When can the details of landscape structure reasonably be ignored? Green (1994) and Fahrig and Pélissier (1988, personal communication) have addressed this question using simulation models. Green considered the effects of habitat connectivity in relation to population and community persistence and concluded that in highly connected landscapes one could treat the entire landscape as a single element (in which case metapopulation theory is not necessary). In less connected landscapes, the effects of the details of the landscape may be possible to treat each element as a separate unit and land the landscape into the percolation threshold (Fig. 4), on the other hand, the explicit spatial arrangement of patches in the landscape and the details of individual movements and patch transition probabilities may become much more important. Fahrig's work suggests that the degree to which the details of landscape structure are important when suitable habitat is abundant and widespread, when individual movement distances are large relative to interpatch distances (i.e., the "grain" of the environment is finer than that of the organism), when movement patterns do not differ greatly among different elements of the landscape (i.e., transition probabilities are roughly equal and high), or when the habitat pattern is equivalent in organisms treat it as such. If this occurs at a broad, population scale, then it is unlikely that metapopulation dynamics will develop. The kind of interplay between local patch structure, individual movements, and local extinction and recolonization that is the essence of metapopulation dynamics would seem to require that the details of landscape structure are important. The percolation threshold and the degree to which the details of landscape structure affect these conditions, attention must be given to the details of landscape structure.

V. METAPOPULATIONS, LANDSCAPES, AND CONSERVATION

The relevance of metapopulation dynamics to conservation issues is treated in detail in many other chapters in this volume, so I will not dwell on it here. If

metapopulations are to be viewed in a landscape context, however, some implications for conservation management be considered. The traditional focus of conservation has been on reserves, and much of the debate about reserve design has dealt with the size, shape, and number of reserves. Reserves have usually been viewed as habitat islands (patches) in a background matrix. Metapopulation theory has become important in conservation biology because it has helped to make patches important and because the widespread occurrence of habitat fragmentation has substantiated it (Wiens, 1995b, 1996b), creating spatial patterns that appear to match those of metapopulations. Metapopulation theory also predicts stability solutions, offering the hope of population persistence in the face of local extinctions.

Habitat fragmentation, however, involves much more than changes in the size and shape of patches. Species may occupy fragmented habitats, but the context of the patches is important. Species may be affected by the context changes, connectivity patterns are altered, and the cost-benefit contours of the landscape shift. Simple island biogeography theory does not deal with such complexity of spatial patterns, and this is one reason why its value in conservation efforts is quite limited (Simberloff and Abele, 1982, 1984; Soderon, 1992; Haila et al., 1993). Species may be affected by the context changes, connectivity patterns are altered, and the cost-benefit contours of the landscape shift. Simple island biogeography theory does not deal with such complexity of spatial patterns, and this is one reason why its value in conservation efforts is quite limited (Simberloff and Abele, 1982, 1984; Soderon, 1992; Haila et al., 1993). Species may be affected by the context changes, connectivity patterns are altered, and the cost-benefit contours of the landscape shift. Simple island biogeography theory does not deal with such complexity of spatial patterns, and this is one reason why its value in conservation efforts is quite limited (Simberloff and Abele, 1982, 1984; Soderon, 1992; Haila et al., 1993).

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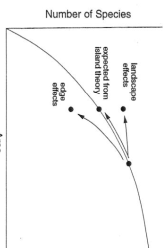


FIGURE 5. The species-area relationship, if the area of a habitat in the landscape is reduced (e.g., by fragmentation), habitat biogeography theory predicts that a new equilibrium number of species that is appropriate to the new habitat area will be reached. Landscape effects (e.g., connectivity, patch size, etc.) may also influence the species-area relationship. On the other hand, edge effects (e.g., low boundary permeability, increased predation mortality in habitat edges) may reduce species number and thus the species-area relationship. The species-area relationship may reflect the effects of each mosaic feature.

The solution to such problems may be to shift from reserve management to "mosaic management," in which reserves are combined with areas that receive varied (and perhaps intense) human use. If one wishes to enhance a metapopulation structure in an area, for example, it may be necessary to manage not only the habitat patches that contain (or could contain) local populations but the landscape between them as well. The management plan for northern spotted owls (*Strix occidentalis caurina*) (J. W. Thomas *et al.*, 1990), rather than evaluating overall landscape connectivity. Proper mosaic management requires that attention be given to all patches and the landscape between them, not just to the patches themselves. This requires a new paradigm in understanding how landscape structure affects movement patterns within and among patches (Wiens, 1999b).

VI. CONCLUSIONS

The main message of this chapter is that landscape structure may often be an important component of metapopulation dynamics. Variations in patch quality in space and time, the form and permeability of patch boundaries, the composition and characteristics of surrounding mosaic elements, and the connectivity among

landscape components may all influence the dynamics of local populations and, especially, the ways in which populations are linked by movements of organisms. The synthesis of landscape ecology with metapopulation dynamics is important.

Although I have emphasized the contributions that landscape ecology can make in developing an understanding of metapopulation dynamics, landscape ecology may also contribute to the development of landscape ecology, in two ways. One is by emphasizing the *dynamics* that occur in a landscape. The spatiotemporal patterns of local extinctions and patch recolonizations create a shifting distribution of local populations, and these patterns create a shifting distribution of landscape ecology. Moreover, an emphasis on these dynamics can draw attention away from the map-based descriptions that characterize some approaches to landscape ecology.

The second way in which metapopulation dynamics can contribute to landscape ecology is by providing a new paradigm to many other areas of ecology. Landscape ecology has developed rather little theory. The field is largely descriptive, in part from the diverse historical roots of the discipline (Fig. 1), but it may also reflect the complexity of landscapes and their linkages. The variety of landscape patterns is virtually unlimited, and thus there is no single mosaic pattern (or small set of patterns) about which theory can be generated (Wiens, 1995a). In contrast, many other areas of ecology have developed a rich theoretical base that can be collapsed into simple patterns of patches and matrix (or so we believe). Perhaps the development of landscape ecology as a predictive rather than a descriptive science requires concepts or theories that link landscape patterns to their consequences. As metapopulation theorists continue to add complexity and realism to simple models, they come closer and closer to developing true mosaic models. Once such models are developed, they may provide a wedge that landscape ecologists can use to develop models of landscape interactions. A linkage of metapopulation theory with percolation theory might be especially fruitful (see With, in press).

Throughout this chapter I have emphasized the importance of understanding movement. Whether or not we understand it, movement is a key component of metapopulation dynamics. Whether or not individuals move among patches, how individuals migrate is, in turn, affected in a myriad of ways by landscape structure. Understanding these effects on movements is of fundamental importance, yet we know very little about movement in an ecological context (May and Studdwood, 1996; Oksanen *et al.*, 1997). Landscape theory will not provide much help here. Instead, we must develop models of movement that take into account the dynamics of individual movements are affected by the explicit spatial patterning of environments. Such investigations can provide the information and insights necessary to bring metapopulation dynamics and landscape ecology together.

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